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GERMINATION OF CEANOTHUS SEEDS[1]

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The many species of ceanothus in California are ecologically diverse, but they occur most frequently and most abundantly on relatively arid sites and where repeated wildfire has been a determinant of vegetative composition. Because of prompt and abundant seedling regeneration after fire (Quick, 1959) and because many or all ceanothus species have nitrogen-fixing nodules on their roots (Quick, 1944), the genus is an important factor in development and conservation of high-quality soil profiles under wildland vegetation. In order to survive fire, seeds "stored" in duff and topsoil must lie in relatively well-insulated positions and be quite obdurate to heat (Quick, 1956).

Most ceanothus seeds will not imbibe water and "plump" in the laboratory unless they are first subjected to some type of heat treatment (Quick, 1935), or to seed-coat scarification. Unplumped seeds cannot germinate because they are dry. Seeds of montane species of ceanothus commonly will not germinate, even if thoroughly plumped, unless an embryo dormancy has been obviated by appropriate stratification treatment; i.e., by continuously-moist aerated storage for some weeks at temperatures slightly above freezing. The present paper reports data from experiments aimed

[1]Facilities for seed storage and culture, stratification and germination were made available by the California Forest and Range Experiment Station, United States Forest Service, in cooperation with the University of California at Berkeley.

TABLE I. EFFECTS OF "STEEP" TYPE HOT-WATER TREATMENT ON GERMINATION OF DEERBRUSH (CEANOTHUS INTEGERRIMUS) SEED

Water temperature degrees C.[1]	Seed sample, weeks stratified at 2.2° C., and age of seeds (years) when cultured. Percent of 40 seeds germinating			
	Q-015 14 2	Q-018 12 ½	Q-018 15 1	Q-087 14 2
70	----	77.5	72.5	----
75	----	77.5	50.0	----
80	72.5	47.5	75.0	100.0
82.5	----	----	60.0	----
85	85.0	87.5	95.0	92.5
87.5	----	----	87.5	----
90	70.0	70.0	67.5	87.5
95	----	70.0	85.0	----
Mean	75.8	71.7	74.1	93.3

[1] Temperature of one liter of water in container at start of "steep" treatment.

at defining optimum laboratory methods for inducing germination of seeds of snowbrush (*Ceanothus cordulatus* Kell.) and deerbrush (*C. integerrimus* H. & A.)[2] Records of seed longevity of these and other ceanothus species are reported also.

The two separate requirements for germination of ceanothus seed of montane species, plumping followed by stratification, are equally important in that either treatment alone is ineffective. Stratification as a prerequisite to germination of seeds of wildland plants is much more frequently encountered than need for special treatment to obviate seed-coat impermeability. However, because seeds must be plumped before they can be conditioned for germination by stratification, methods of plumping will be considered first.

[2] SEED SAMPLES. Seeds used in the experiments were collected from vigorous plants when fruits were fully mature. Collections were thoroughly air dried. Seeds were then extracted from pods by rubbing as gently as possible between two pieces of board. Seeds were sieved, winnowed, recleaned, desiccated over calcium chloride, placed in air tight containers, and stored at 2.2°C. (36°F.).

Collection data for seed lots of *Ceanothus cordulatus* Kell. follow: *Q–155*, August 1937, South Fork Stanislaus River, at ca. 4800 ft. altitude. *Q–156*, August 1937, southwest of Cow Creek Guard Station, Stanislaus National Forest, at ca. 5800 feet altitude. *Q—239*, September 1940, Stinchfield Place, west of Pinecrest, Stanislaus National Forest, at ca. 5500 feet altitude.

Collection data for seed lots of *Ceanothus integerrimus* H. & A. follow: *Q–015*, collected September 1934, same locality as *Q–155*. *Q–018*, July 1935, roadside, state highway 49, south of Grass Valley, Nevada County, at ca. 2500 feet altitude. *Q–026*, August 1931, same locality as *Q–155*. *Q–087*, September 1934, sub-sample of *Q–015* which passed 12-mesh sieve. *Q–113*, September 1936, same locality as *Q–239*. *Q–158*, October 1937, southeast of Cow Creek Guard Station, Stanislaus National Forest, at ca. 6300 feet altitude.

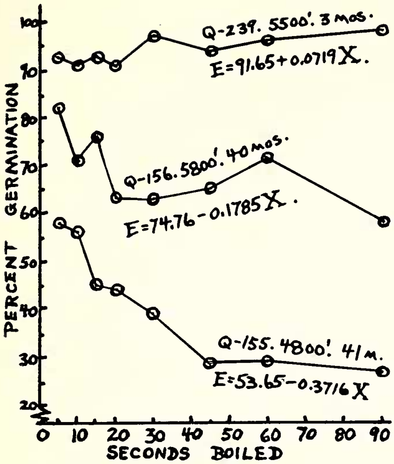

Fig. 1. Boiling water and germination of snowbrush (*Ceanothus cordulatus*) seeds. (Seed collection number, altitude of collection, and age of seed in months.)

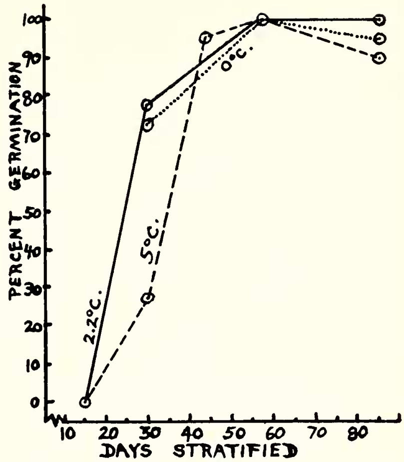

Fig. 2. Temperature of stratification and germination of deerbrush (*Ceanothus integerrimus*) seeds, sample Q–018. (Seeds were placed in 1 liter of water at 85°C. [185°F.] and allowed to cool to room temperature before culturing.)

Hot Water Treatment

Two convenient methods of treating seeds with hot water to increase seed-coat permeability have frequently been used. In the "steep" method, seeds are tossed into a measured volume of water at a given temperature and left in the water until cooled to room temperature. In the boiling-water treatment, seeds are vigorously boiled in water (212°F.) for a given length of time. After the allotted period of boiling, the seeds are soused in an excess of cold water and then cultured.

Table 1 reports results of treating four lots of deerbrush seeds in hot water by the steep method. The volume of water in all tests of this series was one liter (1.06 quarts). Temperature at start of treatment varied from 70°C. (158°F.) to 95°C. (203°F.). All cultures were of 40 seeds, and all were stratified at 2.2°C. (36°F.) after the hot-water treatment. The steep treatment obviously is satisfactory for removing impermeability of deerbrush seed-coats.

Boiling water also will condition ceanothus seeds for successful stratification and germination (Quick, 1935). A treatment somewhere between a few seconds and perhaps 10 minutes might be expected to be the optimum period in boiling water. This optimum treatment could be expected to vary with different species, and with differences in maturity, age, and condition of seed of a single species.

Figure 1 presents data resulting from treatment of three samples of snowbrush seed (*C. cordulatus*) in boiling water. The objective was to determine if optimal treatment with boiling water lay between 5 and 90

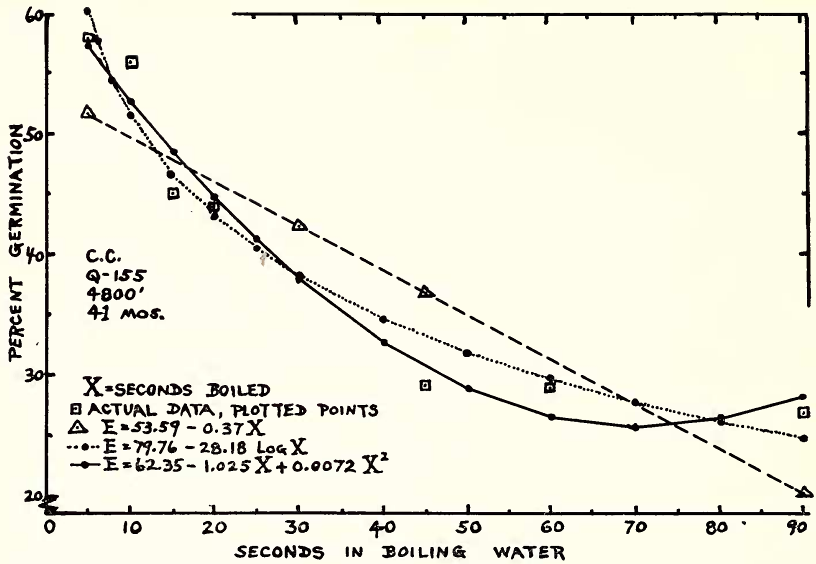

FIG. 3. Statistical generalization of germination data from snowbrush (*Ceanothus cordulatus*) seeds boiled in water, showing curves for straight-line regression, logarithmic regression, and multiple regression. (Seed collection Q–155, 4800 feet altitude, age 41 months.)

seconds. Each culture consisted of 100 seeds. Seeds were treated in Berkeley at an altitude of about 125 feet by tossing them into vigorously boiling tapwater and by pouring the boiling water and the seeds into excess cold water at the end of treatment. Seeds were planted in autoclaved river sand, left at room temperature a few days to plump, then stratified at 2.2°C. for 94 days, and finally germinated in the greenhouse for 5 weeks.

No obvious optima appear on the graphs of figure 1. The best period of treatment in boiling water for sample Q–239 at time of testing may have been more than 90 seconds. In contrast, the other two lots appeared to have very short optimal periods of boiling.

Some tests on deerbrush seeds (*C. integerrimus*) indicate that very short periods of boiling will condition only part of the seeds of a sample for germination. For example, seeds of collection Q–087 (age 26 months) were boiled for various short periods. Final germination was as follows: boiled 4 seconds, 20% germination; 8 seconds, 78%; 16 seconds, 63%; 32 seconds, 68%; and 64 seconds, 73% germination. The four-second treatment obviously was too short to be effective on the majority of seeds of this two-year-old collection. Likewise seeds of sample Q–026 at age of 28 months were boiled for short periods, stratified at 2.2°C. for 102 days, and germinated in the greenhouse. Germination follows: boiled 30 seconds, 60% germination; 1 minute, 76%; and 2 minutes, 64% germination. Most lots of snowbrush seed seem to be adequately treated by shorter periods of boiling than deerbrush seeds. No very short and obvi-

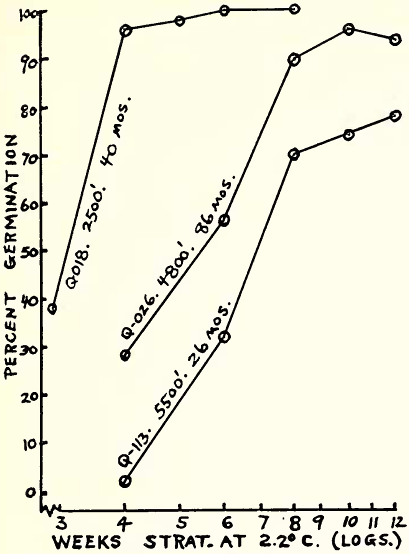

FIG. 4. Length of stratification and germination of deerbrush (*Ceanothus integerrimus*) seeds. (Seed collection number, altitude of collection, and seed age in months.)

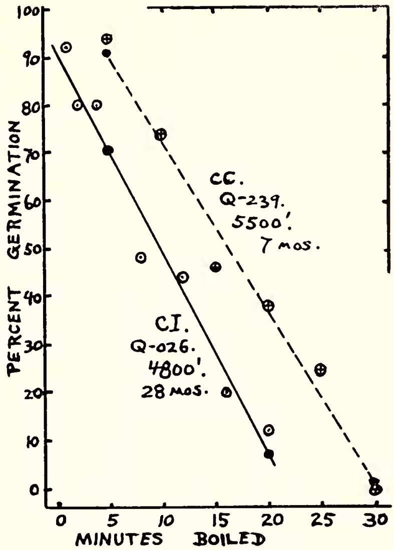

FIG. 5. Germination of ceanothus seeds after long boiling in water. (Species of ceanothus, seed collection number, altitude of collection, and age of seed in months.)

ously inadequate treatments of snowbrush seeds with boiling water, such as described above for deerbrush seeds, have been observed.

Statistical Generalization

When small lots of ceanothus seeds of a single sample are boiled for various short periods, then stratified and germinated, a graph of results commonly appears to fit a curve rather than a straight line (fig. 1). From theoretical considerations of the effects of boiling water on horny seed coats, an exponential scale on the time axis of a graph would be expected to fit the data better than an arithmetic scale. This generalization can be conveniently handled in linear regression analysis by using logarithms of time units rather than time units as such (Snedecor, 1938, pp. 308–312). Another common method of "fitting" a curve is to add, as a second variable, the square of the independent variable—in this case the square of the time units (Snedecor, 1938, pp. 313–316).

Figure 3 graphs data resulting from eight cultures of boiled snowbrush seed. Plotted first in this figure is the straight-line regression in which time of boiling is handled arithmetically as number of seconds. Also on the graph is a logarithmic regression, computed by linear regression methods, in which time (the independent variable) was the common logarithm of seconds boiled. The third line on the graph is the multiple regression curve in which two time variables, (1) seconds boiled, and (2) square of seconds boiled, were used.

The straight-line equation appears to be an oversimplification of the data involved. The multiple regression equation in which the square of seconds boiled was added as a separate variable is not a valid generalization because it predicts a minimum germination percentage at about 70 seconds of boiling and a steadily rising germination percentage after 70 seconds. The logarithmic transformation appears to be the best generalization of the three presented and will be used hereafter whenever a straight-line relationship is not considered adequate.

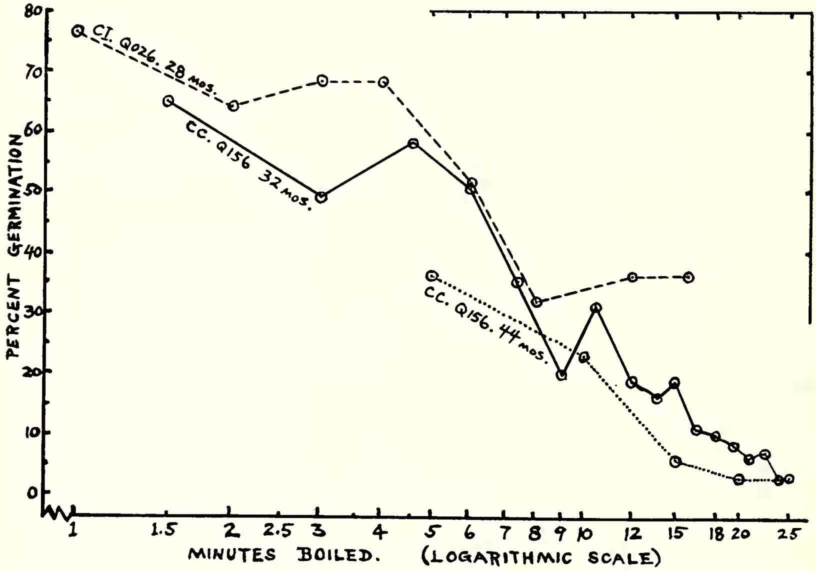

Fig. 6. Additional tests on long-boiled ceanothus seeds. (Species of ceanothus, seed collection number, and age of seed in months.)

Stratification Time and Temperature

A reasonably effective temperature and period of stratification must be known before conclusions about effects of other variables in germination of ceanothus seed can be considered precise. Work reported by Quick (1935) indicates one treatment (2.2°C. for 3 months) that seems generally effective, but offers no comparison with other time-and-temperature combinations. Figure 2 reports results of a series of stratification tests on deerbrush seed of sample Q–018. Obviously any one of three stratification temperatures will satisfactorily condition water-permeable deerbrush seed of this lot for germination. Other experiments have shown that snowbrush seeds react similarly, but commonly are best stratified at 2.2°C. or 0°C. rather than at 5°C.

Differing severities of hot-water treatment might conceivably change the time-and-temperature reactions of ceanothus seeds to subsequent

TABLE 2. GERMINATION OF OLD CEANOTHUS SEEDS

Seed Collection No. (Quick)	Species of *Ceanothus*	Approximate Collection Altitude, Feet	Seed Age, Years and months	Seeds per culture	Seeds Boiled, Seconds	Stratification, Days	Germination, Percent
014	*C. arboreus* Greene[1,2]	225	20-5	50	6	none	38
370	*C. arcuatus* McMinn	6000	9-5	50	20	90	66
155	*C. cordulatus* Kell.	4800	15-4	100	10	108	71
156	" " "	5800	15-4	100	10	108	87
239	" " "	5500	12-3	100	10	108	90
317	" " "	5800	13-4	100	20	90	81
318	" " "	6600	13-3	100	20	90	86
056	*C. cuneatus* (Hook.) Nutt.	2700	17-5	100	10	98	98
024	*C. divaricatus* Nutt.	----	19-6	100	5	108	46
183	*C. impressus* Trel.[1]	400	17-7	25	5	none	88
026	*C. integerrimus* H. & A.	4800	24-4	100	20	90	90
015	" " "	4800	21-3	100	20	90	100
087	" " "	4800	21-3	100	20	90	93
018	" " "	2500	20-5	100	20	90	93
158	" " "	6300	15-3	100	10	108	98
238	" " "	5500	12-3	100	10	108	97
057	*C. lemmoni* Parry	2700	17-5	100	10	108	96
247	*C. prostratus* Benth.	5800	12-5	80	10	108	100
028	*C. sorediatus* H. & A.[3]	750	22-1	100	10	73	85
017	" " "	800	17-5	100	10	86	96
025	*C. spinosus* Nutt.[2]	250	19-4	66	5	108	93
246	*C. velutinus* Dougl.	4300	12-4	100	10	108	92

[1] *C. arboreus* and *C. impressus* not stratified prior to germination.
[2] Seeds from landscape planting.
[3] *C. sorediatus* stratified at 5°C. (41°F.), all other species at 2.2°C. (36°F.).

stratification. However, two series of cultures of deerbrush seed, sample Q–018, one of seeds boiled for 20 seconds and the other for 70 seconds, reacted the same to stratification, insofar as could be told from inspection of the data.

Quick (1935) found that requirements for optimal stratification of ceanothus seed apparently varied among the species in relation to the altitude at which the species commonly grew. Results from series cultures of three collections of deerbrush seeds from different altitudes are summarized in figure 4. Deerbrush seeds from lower altitudes appear to respond progressively to shorter periods of stratification.

Tolerance to Boiling Water

Immersion in boiling water for 10 to 20, or perhaps 30 seconds will satisfactorily condition most ceanothus seeds for germination, if subsequently the seeds are adequately stratified. The limit of tolerance of both deerbrush and snowbrush seeds to boiling water was tested in Berkeley by individually boiling subsamples from 1 to 20 or 30 minutes. Figure 5 graphs the results from long-boiling treatments on one lot of deerbrush seed, Q–026, and one of snowbrush seed, Q–239.

The regression equation for the deerbrush series of treatments is $E = 91.64 - 4.214X$ ($r = 0.982$), where X is simply minutes boiled. This equation predicts that on the average 4.2 percent of germination is lost for each minute the seeds of lot Q–026 are boiled. The corresponding equation for the snowbrush series is $E = 108.67 - 3.571X$ ($r = 0.989$). The regression line for deerbrush seeds crosses the time axis—zero germination—at 21.75 minutes, and for snowbrush seeds at 30.43 minutes! These two tests indicate that snowbrush seeds may be more resistant to boiling water than deerbrush seeds. Additional tests of resistance to boiling water were made. Results are presented in figure 6.

It is amazing that ceanothus seeds can stand such prolonged periods of boiling. The seed coats presumably exclude water from the seed proper; the embryo and endosperm are in effect subjected to dry heat for the period of the boiling. It is unknown whether death of over-boiled seeds is due to the effects of dry heat on embryo or endosperm or to the final penetration of boiling water or steam through the seed coats. Effects of dry heat on seeds from which coats have been removed have not been determined.

Seed Longevity

In an ecological sense many ceanothus species are pioneer plants and therefore might be suspected of having durable, long-lived seeds. Seeds of some species are known to be generally distributed in the duff and soil of Sierra Nevada forests (Quick, 1956). Actual germination tests of old ceanothus seeds would be of some ecologic interest. Table 2 presents a few records of longevity for seeds of known age.

Many factors may condition results of germination tests on old seeds, and high levels of consistency between species and collections, ages and individual tests are not necessarily expected. Additional tests will be required to define maximum seed life under the pertinent conditions of seed collection, handling and storage. The reported data, however, confirm the fact that seeds of many ceanothus species are long-lived.

Berkeley, California

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